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SHORT COMMUNICATION

Mesothelae have venom glands

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Abstract. Although venom glands were described for the Mesothelae many years ago (Bristowe & Millot 1933), a more recent monograph (Haupt 2003) denied the existence of such glands in the Mesothelae. Our morphological studies of nine different species of *Liphistius* demonstrated the presence of venom gland openings on the cheliceral fangs in all of these species. Also, we observed a small venom gland in the anterior portion of the cheliceral basal segment. The possibility that venom glands may be lacking in adult males is discussed. The presence of venom glands in the Mesothelae indicates that this is a plesiomorphic character of all Araneae.

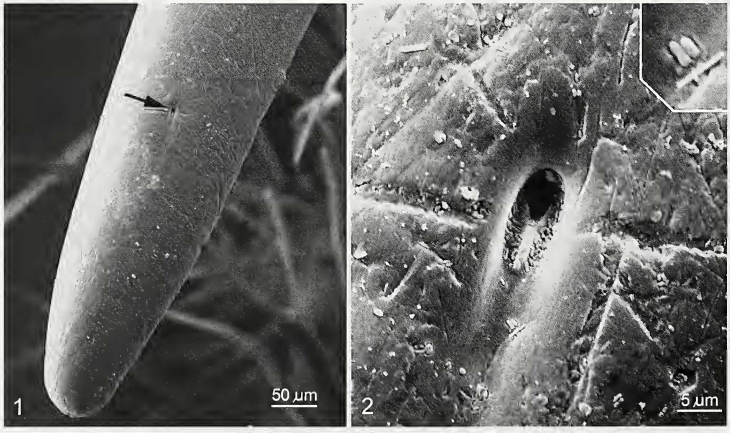
Keywords: *Liphistius*, venom glands

A venomous bite is a typical feature of most spiders. Only members of the family Uloboridae lack venom glands (Millot 1931), but most likely they lost them secondarily. Recently it was claimed that the ancient Mesothelae (Liphistiidae) also lack venom glands (Haupt 2003). This claim contradicts an earlier study in which small venom glands were described for *Liphistius desultor* (Bristowe & Millot 1933). The aim of the present study was to examine a number of species of *Liphistius* to check whether venom glands are present or not. Our first step was to inspect the cheliceral fangs with a scanning electron microscope to see if they have venom gland openings, as is generally the case in spiders. In a second step, we dissected some chelicerae under a binocular microscope in order to find the venom gland itself.

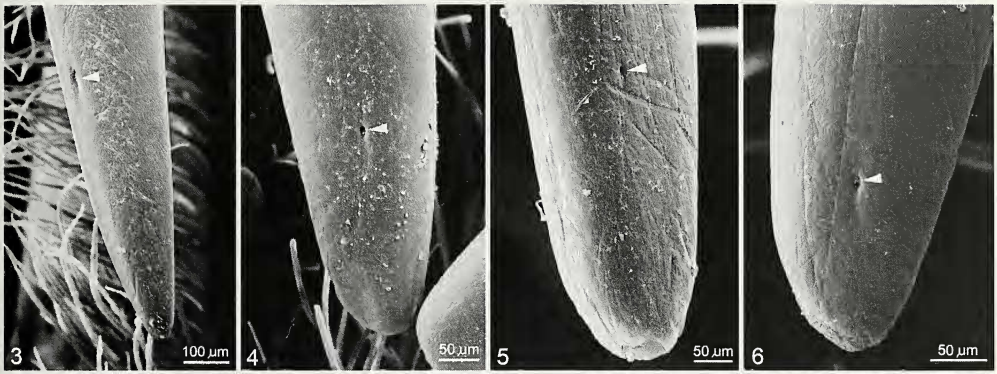
Most specimens were provided by Dr. Peter Schwendinger of the Muséum d'histoire naturelle in Geneva, Switzerland. Specimens fixed in alcohol or exuviae of the following nine species were at our disposal: *L. bicoloripes* Ono, 1988, *L. bristowei* Platnick & Sedgwick, 1984, *L. dangrek* Schwendinger, 1996, *L. desultor* Schiødte, 1849, *L. endau* Sedgwick & Platnick, 1987, *L. malayanus* Abraham, 1923, *L. niphanae* Ono, 1988, *L. sunatranus* Thorell, 1890, und *L. yamasakii* Ono, 1988. Isolated chelicerae were dehydrated in alcohol and acetone and then transferred to HMDS (Hexamethyldisilazane; Nation 1983) for 10 min to avoid shrinkage, before air drying on filter paper. After being sputtered with gold, we examined them from different angles in a Zeiss DSM 950 scanning electron microscope (SEM) at 15 kV.

We performed dissections of chelicerae placed in alcohol using watch maker forceps and micro-scalpels (razor blade fragments). Isolated venom glands were studied under various illuminations with a Leitz light microscope; best results were obtained under polarized light.

Since venom glands in orthognath spiders are relatively small and thus difficult to find, it seemed easier to begin by simply looking for any pore openings of possible glands near the tip of the cheliceral fangs. In most labidognath spiders, these openings are rather large



Figures 1, 2.—Cheliceral fang in *Liphistius bristowei*. 1. Ventral view; the opening of the venom gland (arrow) is barely visible and lies far away from the tip of the fang. 2. Higher magnification of the pore shows a slipper-shaped opening. Note the tiny rods inside the pore which represent bacteria (*Inset*).



Figures 3–6.—Ventral view of cheliceral fangs in different *Liphistius* species; the arrowhead points to the opening of the venom gland. 3. *L. desultor*; 4. *L. niphanae*; 5. *L. yamasakii*; 6. *L. endau*.

and are situated on the backside of the cheliceral fangs, close to the tip. In orthognath spiders (theraphosids), they lie in a different location, namely at the convex side of the cheliceral fang and can only be seen if viewed directly from the ventral side. We found that this is also the case in the Mesothelae (Foelix & Erb 2010). Two other factors make these openings difficult to detect: (1) they lie relatively far away from the tip of the cheliceral fang, usually 300–400 µm (Fig. 1), and (2) they are very small, measuring only 5–10 µm in diameter (Fig. 2). However, after having found such a pore opening on one chelicera, we always found it possible to identify the corresponding pore (same location, same size) on the other chelicera. This was true for all the species examined in this study (Figs. 3–6). Only in a few cases were we unable to detect these openings. Whether this is really "evidence for absence" is hard to say, but we offer a possible explanation in the Discussion.

Finding the venom glands in *Liphistius* also presents a challenge. The entire basal segment of a chelicera is packed with muscle tissue and in fresh material we were unable to locate any gland, despite knowing where to expect to find it. We were more successful, however, when using alcohol-fixed material. There the muscle tissue forms solid bundles of individual muscle fibers which can be plucked out in a stepwise fashion with watch maker forceps. Only when almost all muscle fibers have been removed, does the venom gland gradually appear, right behind the insertion of the cheliceral fang into the basal segment (Fig. 7). The body of the gland is about 1.5 mm long and 0.5 mm wide and is surrounded by a "spiraling" muscle layer. (Fig. 8). Under polarized light, a distinct herring-bone pattern becomes visible, caused by parallel muscle fibers arising obliquely from a longitudinal line ("backbone"). Actually, the muscle fibers do not really spiral around the body of the gland but several rectangular muscle cells are arranged serially and form a kind of belt. At higher magnification these muscle fibers show a marked cross-striation (Fig. 9) which indicates that they can contract voluntarily. The gland itself lies underneath that muscle layer but no details could be seen in our whole mount preparations. We found the venom gland in the chelicerae of a female (*L. bicoloripes*) but not in the single male specimen (*L. dangrek*) that we had available for dissection, so we cannot be sure whether this absence is typical for all male *Liphistius* spiders.

Our study indicates that Mesothelae (*Liphistius* species) do possess venom glands since we could detect venom gland openings on the cheliceral fangs in nine species. We also found the venom gland itself, at least in the female. This is in accord with an early publication by Bristowe & Millot (1933), in which Millot described a small venom gland in *L. desultor*, and also included a detailed sketch of its location and its microscopical structure. Millot's main conclusion was that the venom gland in *Liphistius* is morphologically identical to the venom gland in theraphosids. In contrast, in his monograph on Mesothelae, Haupt (2003) stated that "Mesothelae lack such venom glands," and "there is no pit on the fang indicating the opening of the gland." The latter claim can now be refuted, as our SEM pictures definitively show the presence of such a pore in all the nine species examined (Figs. 3–6). The fact that Haupt (2003) did not see any pore openings in the light microscope can perhaps be explained by the thick cuticle of the cheliceral fang and the tiny size of these pores (5–10 µm). It is more difficult to understand why his SEM pictures do not show any pore openings either, although the orientation of the cheliceral fang seems correct (ventral side up). However, the magnification he used in the SEM was rather low and the small pores could be clogged. There is another possible explanation: perhaps he was looking only at adult male chelicerae, which may lack such pores. Since *Liphistius* males are very short-lived and hardly capture any prey as adults (Schwendinger, pers. comm.), it could well be that they have reduced or lost their venom glands with their final molt. It is known from other spiders that the adult males may lose certain characters with their last molt, [e.g., male cribellate spiders lose their cribellum and calamistrum, and male orb weavers lose their triad spigots that normally produce the sticky capture thread (Foelix 2011)]. What needs to be done in future studies is to focus on adult male *Liphistius* and check specifically for the presence or absence of venom glands.

Clearly, Mesothelae have venom glands, at least in the female and juveniles. Their general presence in *Liphistius* implies that this is an ancient (plesiomorphic) feature and not an apomorphic character of the Opisthothelae, as suggested by Haupt (2003).

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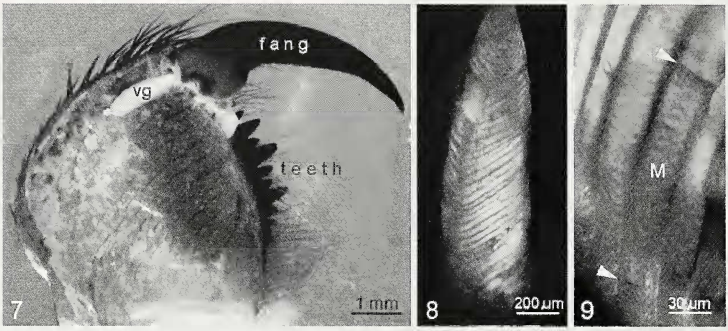

Figures 7–9.—Venom glands in *Liphistius bicoloripes*. 7. Dissection of a chelicera showing the location of the venom gland (vg) behind the articulation of the fang; all muscle tissue has been removed from the basal segment of the chelicera. 8. Isolated venom gland under the microscope using polarized light; muscle fibers surrounding the gland are arranged in a herringbone pattern. 9. Higher magnification view of the muscle layer reveals the cell borders (arrowheads) of adjacent muscle cells (M) and the distinct cross-striation of the cytoplasm.

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